Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

# PROBLEMS OF FLORAL DOMINANCE IN THE OPEN SEA[1]

W. E. Allen

*Biologist, Scripps Institution, La Jolla, California*

When one suggests a comparison of plant life on land with that of the open sea, the enormous and obvious differences in the conditions of existence come obtrusively to mind. The land flora appears to be peculiarly a border flora set fixedly into the surface of a solid substratum and projected outwardly into a gaseous stratum. Its contact with water, the essential fluid medium, is not much in evidence. Two such diverse media as air and soil offer vast possibilities for variability in conditions of existence, possibilities very considerably increased by the relation of both to the necessary fluid. As a consequence we find a complexity of conditions and of interrelationships which is most impressive. The slightest irregularity in land surface usually has profound and incalculable influences on the character of the plant population of its vicinity through changes in details of its contact with the atmosphere and through changes in the incidence of light, range of temperature and capacity for retaining water. Add to this the infinitely varied structural details of the soil itself and we get an almost incomprehensible total.

With such complexity of conditions the open sea seems to offer material for contrast rather than for comparison. The activities of organisms are confined to one medium of the three already mentioned, the fluid medium, the most important biologically, it is true, but none the less giving a greatly simplified physical relationship. Furthermore, on account of the fluid character of the medium and the ease of diffusion in it, one may easily suppose that its structural features are uniform and invariable, at least over large areas. It also appears that its great mobility tends to eliminate those highly influential irregularities of surface so evident on the solid earth.

There are, however, fundamental similarities which appear on closer study. Cyclical changes in temperature and light are no less important in the sea than on land, though often less extreme and abrupt. Ocean currents, up and down, north and south, east and west, and to all intermediate directions are constantly causing changes in conditions quite similar to many of those which occur on land as a result of irregular soil surface and very frequent readjustments of the relationships of the solid and gaseous strata. It is also true that many shifts and changes in the superimposed atmosphere affect living conditions in the sea just as markedly as on land.

---

[1] Presented before the joint meeting of the Ecological Society of America and Western Society of Naturalists at Seattle, Wash., June 18, 1920.

All things considered, it seeems reasonable to assume that the basic conditions of plant life in the sea are similar to or identical with those of plant life on the land. The removal of the direct physical influence of the land mass with its infinite variety of surfaces and its innumerable differences in soils does much toward simplifying the problems of life and laying bare the modes of operation of various factors involved. For this reason plant life in the open sea ought to make strong appeal to the plant ecologist. This is still more true because a good many people are disposed to say that life originated in the sea and it is there that we may hope to gain direct knowledge of original sources. The evident difficulties of relative inaccessibility, invisibility, and high expense, while formidable, are not insuperable bars to investigation. The field is practically untouched. My own wish in presenting this paper is to turn serious attention to work in it. The study of the ecology of land plants has progressed so far and so favorably in recent years, in spite of the intricate conditions, that it seems especially desirable to bring up our knowledge of marine ecology for purposes of supplement and comparison if for no other.

As illustrative of these things we may give brief attention to problems of dominance. So far as land plants are concerned, we are fairly well informed as to the general conditions of dominance, both temporary and continuous. The first condition is one of foothold since it is manifestly impossible for an organism dependent on absorption of dissolved substances to get sufficient sustentative materials if subject to constant shifting of contacts. Hence we find that newly exposed rock surfaces or freshly abraded soil surfaces are first occupied by minute cryptogams favored in such a situation by their wide dissemination of spores, rapid multiplication, small size, and powers of adhesion.

The second conditions of dominance is hardihood or power of endurance. The microscopic cryptogam gives way to the lichen with its superior equipment for resisting desiccation, extremes of temperature, light, mechanical injury and accumulation of its own wastes. Lichens in turn give way to mosses or still higher cryptogams with larger bodies which give opportunity for regional differentiation including various types of protective coverings. Similar changes continue to occur until some one of the higher flowering plants overcomes competition on that area.

The third condition of dominance is assimilative capacity. Given a foothold and effective powers of resistance, the plant which does best is the one which can most rapidly use available nutrients under the existent conditions. The microscopic alga makes relatively little use of its rock substratum. Nor does the lichen do much more, but the higher plants show more and more ability to use the rock substance itself as well as the accumulated remains of their dead predecessors. This ability to use a wide variety of foods gathered in many different ways plays no small part in the success of the higher plants.

The fourth condition of dominance is reproductive capacity. Other things being equal, it is very easy to see that the plant which can most rapidly increase its numbers is going to drive out those of similar habit.

The fifth condition of dominance is freedom from attack by animals. We are all familiar with pasture lands in which occur large areas covered with plants which are protected by spines, or bad taste, or noxious qualities, and so are enabled to spread over ground formerly occupied by closely cropped plants of edible character.

It is probably sufficiently obvious to all of you that this arbitrary list of conditions determinant of dominance is arranged solely for the convenience of this discussion. It is also doubtless apparent that the microscopic plants of the open sea are most readily comparable in character and habit with the microscopic pioneers of the barren rock. Both types are very small, very prolific and very responsive to changes in the surrounding media.

Just which microscopic alga is to assume dominance or exclusive control of a new rock area depends upon presence or absence at a given time, upon relative numbers, upon vigor and upon adaptability of the species capable of such an existence. The temporary dominant upon a new rock may be such merely because the winds or rain waters have carried it down from a higher level at a time when cloudy weather prevented too much dryness and heat from injuring it. It could not have competed originally against similar plants belonging to that level and it is soon superseded by the more appropriate plant when the latter is introduced by some carrier. This is especially true when the normal temperature of the lower level returns, bringing failure to the one and success to the other.

Similarly the temporary dominant in a given ocean area may be such merely because a powerful storm current has carried it in with a mass of water of higher salinity which has changed the physical conditions of the water of that area for several days. It could not have competed with the plants usually found in that vicinity at normal salinity and it is rapidly displaced by them when normal salinity is restored through change in currents or through diffusion.

My reason for first calling attention to an unusual combination of circumstances rather than to the normal is because I want to emphasize the difficulty of interpreting dominance or any biological phenomenon without continuous observation. A casual visitor to the region might conclude that the temporary microscopic flora on the new rock was characteristic and an infrequent collector of phytoplankton might conclude that a diatom found dominant at the very brief time and space of his collecting was also characteristic. In the first case an experienced observer might be able to check his observations by a general view of the surrounding country. No such view is available for use in the sea both on account of the high mobility of the fluid medium and because of the extremely limited range of vision through it. It is especially necessary then that we should be cautious about reaching conclusions from disconnected observations or from single or limited series of continuous observations.

Although, as I said before, we have not yet gone very far toward gaining a clear understanding of biological conditions in the sea, a very great deal of suggestive and stimulating work has been done. From this we get a good deal of light on phenomena of dominance which is useful for tentative conclusions. In the light of present knowledge let us examine the five conditions of dominance which I have arbitrarily listed.

At first thought the first condition, that of foothold, does not apply in the sea. Most diatoms and dinoflagellates live in the upper strata of water which are more or less continuously agitated and shifted. Being entirely surrounded by its necessary fluid which is essentially the same in composition over areas incomparably greater than its own dimensions, it seems to be a matter of indifference whether or not it retains a given position. Within very small geographic limits this may be true but relatively to its surroundings it is not true. For example, it is fairly well known that many of these organisms are very sensitive to changes in salinity, light, density, and temperature. Some, then, are well qualified to live near the surface of the sea, within the upper five meters perhaps. This necessity for living in the five meter stratum of water is somewhat comparable to the necessity for the small alga to adhere to the rock. More or less elaborate devices are developed to secure flotation for the marine plants at the proper level of density, temperature, etc. Flotation devices are, then, somewhat similar to fixation devices and we find them about equally important in their effects on aquatic organisms.

The condition of hardihood is probably as important in the sea as on land. We have some interesting light on that point from some experiments performed at Plymouth Laboratory in England in which many different kinds of diatoms were cultivated for many generations. In reporting the results of work from 1905 to 1909 the experimenters list eighteen species of diatoms which had been successfully cultivated for long periods of time. In the case of *Skeletonema costatum* continuous culture had been maintained for a period of four and one half years and it was still vigorous. When placed in mixed cultures, however, it was not able to survive. In fact under laboratory conditions none of the strictly oceanic forms could hold their own with the inshore forms when placed in mixed culture. Some oceanic forms were more readily overcome by presence of bacteria than were others, in cases where sterilization of culture media was not wholly successful. It is definitely recorded that no species of diatom, except one inshore species of

*Nitzschia*, was able to maintain itself against the encroachments of a species of *Pleurococcus* sometimes admitted to the cultures. One of the very interesting points developed by the series of experiments was that inshore forms which displaced oceanic forms in cultures were never found dominant to oceanic forms in nature though a few of them were always present. Evidently the artificial conditions of the culture were much more easily endured by some forms than by others.

As to the influence of assimilative capacity we have little or no direct evidence so far as the phytoplankton is concerned. There is, however, no reason to suppose that differences which do occur can be any less important than in the case of land plants. The same thing is to be said about reproductive capacity. The two conditions are so closely related in the case of microscopic plants that it is almost impossible to separate them. The Plymouth Laboratory experiments showed that water from the open sea when placed in culture without segregation of species always led to early exteme dominance of *Skeletonema costatum*. As *Skeletonema* died out the others increased. Such results of experiment point to the probability that *Skeletonema* excels both in assimilative capacity and rapidity of reproduction.

Concerning the question of freedom from attack by animals, we must again note that there is scant evidence. The best evidence which we have is afforded by the fact that certain fish such as mackerel are not found in a given area of water when certain diatoms or dinoflagellates are excessively numerous. In this connection we are again able to make some use of Plymouth Laboratory experiments. These showed very clearly that certain diatoms were much superior to others for use as food in rearing various marine larvae. In fact one might say that *Nitzschia closterium* finally came to be regarded as the standard food for most of these animals and for certain copepods. In the case of *Calanus finmarchicus* it appears, however, that the excretions of the animal may sometimes so stimulate and support the development of the plant that it is able to increase rapidly in spite of the destruction of vast numbers. It is hardly possible that this result could be reached in nature because the *Nitzschia* would have to meet general competition as well as the destructive feeding of the copepod.

Turning from general discussion of general factors, let us briefly consider one or two specific cases and some specific factors. One of the dominants in our San Diego region which has interested me very much is *Nitzschia seriata*. This is because it was found very distinctly dominant in the region near Santa Barbara Island (forty miles off shore) in the summers of 1917 and 1918, and it was also found continuously dominant at our pier through February and a part of March of this year. I have as yet no clue to the cause of dominance at two such diverse situations and seasons. I can only guess that it may be due to the influence of some animal.

*Chaetoceras curvisetum* shows signs of dominance in April, though I have not yet carefully examined the material. It has been found dominant at about this season before. Such dominance may be explained by the seasonal increase of light connected with other factors yet undetermined.

*Chaetoceras criophilum* is apparently a typical oceanic dominant in our offshore region in June and July. In this case my guess would be that flotation and vigor of growth are amongst the most prominent factors in dominance aside from the intricate combination of conditions which goes to make up the seasonal influence. By the work of Dr. McEwen hydrographic conditions in our region have been shown to be distinctly variable and subject to sudden changes of a good deal of magnitude. Much of this is caused by upwelling and other water currents due to irregularities of bottom and shoreline and to general meterological conditions. We are thus enabled to see that there are frequent and rapid changes of conditions affecting dominance and a corresponding difficulty for any one plant to maintain long continued dominance in a given area.

The fact that we frequently find swarms of diatoms or dinoflagellates almost exclusively occupying areas varying from a few square yards to some scores or hundreds of square miles, leads to the view that dominance is very often based on ability of a particular species to not only grow and multiply excessively under given conditions, but also to develop some offensive secretion or deterrent activity which enables it to drive out and displace other plants.

One of the most prominent features of plant life in the open sea is the shortness of periods of dominance. Sometimes a dominant may be carried entirely away from a favorable area by a wide sweeping storm current. In other cases it may be rapidly destroyed by the cold water of an upwelling current. In still other cases, its numbers may be rapidly depleted by predatory animals. Increased sunlight may retard one plant while stimulating another. In any case it means a new shuffling of the cards in which the conditions of dominance may or may not have the same relative values in determining the success of certain species as they had had before. Since a paper of this sort can hardly be considered up to date without at least some mention of hydrogen-ion concentration, I may say also that a change in that concentration is likely to affect one plant more than another and so to initiate a reversal of dominance.

If I have done nothing more I hope that I have been able to show that these problems are fascinating and important and that concerted effort may do much toward solving them.